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Distribution of *Alternaria* species among sections. 2. Section *Alternaria*

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Abstract — Among several groups of small-spored *Alternaria* species, *A.* sect. *Alternaria* (containing the generic type) has been found to be isolated, based on phylogenetic as well as morphological data. Molecular phylogenetic data confirm inclusion of twenty-one species in this section besides the type species. Examination of additional material, conforming to the morphological description for the section but not as yet phylogenetically characterized, allow confirmation of an additional 37 species. All 59 species are listed, and an emended description of *Alternaria* sect. *Alternaria* is presented.

Key words — *Alternaria alternata*, *A. herbiphorbicola*, *A. gomphrenae*, *Pseudoalternaria*

Introduction

The genus *Alternaria* Nees is a large taxonomic group that comprises approximately 280 species (Simmons 2007). A series of large-scale works has attempted to resolve the phylogeny of *Alternaria* and other alternarioid hyphomycetes by employing more than ten different genomic loci (Pryor & Bigelow 2003; Hong et al. 2005; Runa et al. 2009; Lawrence et al. 2012, 2013, 2014; Woudenberg et al. 2013). Several well-supported phylogenetic lineages have been revealed within the alternarioid hyphomycetes, resulting in several taxonomic novelties. The genus *Alternaria* was divided into eight taxonomic sections by Lawrence et al. (2013). Presenting an alternative concept, Woudenberg et al. (2013) collapsed all alternarioid hyphomycetes into one genus, *Alternaria*, with 24 sections, 11 of which referred to *Alternaria* sensu stricto.

All works support a monophyletic status of a particular *Alternaria* group, one of several groups having members with catenate, small-spored conidia.

Both research teams (Lawrence et al. 2013; Woudenberg et al. 2013) agreed that based on both molecular phylogenetic and morphological data, this group (including the type species *A. tenuis* [= *A. alternata*]) should be treated as a well-defined section. This section, which contains the type of the genus, is an autonymous section that must repeat the generic name as its epithet, *Alternaria* sect. *Alternaria*, and is not followed by any author citation (McNeill et al 2012: Art. 22.1). Lawrence et al. (2013) were mistaken in presenting this section as a sect. nov. with themselves as authors. Woudenberg et al. (2013), who repeated the erroneous attribution to Lawrence et al., misspelled the epithet as "*Alternata*".

Lawrence et al. (2013) referred thirty-one strains to *A.* sect. *Alternaria.* However, six strains belonged to *A. gossypina*, *A. grisea*, *A. grossulariae*, *A. lini*, *A. maritima*, or *A. nelumbii*, species denoted by Simmons (2007) as taxa that are not distinguishable morphologically from other small-spored *Alternaria* species, that lack isolates from identified field material, that were considered as INCERTAE SEDIS, or whose only isolate(s) sporulate inadequately. Another strain (CBS 1010.26) is labelled with the invalid name "*Alternaria iridis*", referring to *Macrosporium iridis* Cooke & Ellis, which is a *Stemphylium* (Simmons 2007: 722). Strains of three other species used by Lawrence et al. (2013) — *A. malvae, A. rhadina*, and *A. tomato* — were not authentic or representative. Strain CBS 595.93 was deposited as "*A. rhadina*" by the species author, E.G. Simmons, but he subsequently reported that this strain was mislabelled and did not represent an authentic *A. rhadina* (Simmons 2007: 512). Here I regard it as representing an unnamed *Alternaria* species and exclude it from my list.

An isolate of *A. tomato* (CBS 114.35) clustered in a clade referred to as *A.* sect. *Alternaria* (Lawrence et al. 2013). However, the credible species description in Simmons (2007) suggests that this species resides better in *A.* sect. *Porri*. According to Simmons (2007: 356), no correctly identified *A. tomato* isolates are known. Hence, we suggested that *A. tomato* sensu Simmons belongs in *A.* sect. *Porri* (Gannibal 2015).

Lawrence et al. (2013) placed *A. resedae* CBS 175.80 in *A.* sect. *Alternaria*. The molecular phylogenetic analyses by Woudenberg et al. (2013) placed the representative strain of *A. resedae* Neerg. CBS 115.44 in *A.* sect. *Cheiranthus*. Earlier Simmons (2007) had suggested that this name is a synonym of *A. septorioides* (Westernd.) E.G. Simmons in *A.* sect. *Brassicicola*. Obviously CBS 175.80 and CBS 115.44 belong to different species and most likely they do not both correspond to the description used by Simmons. Hence I do not recommend using the name *A. resedae* until a species study has been completed.

Based on ITS1-2 rDNA sequence analysis Hoog & Horré (2002) included 33 strains of 7 species in group *alternata*. Apart from the well-studied species *A. lini*, *A. mali* and *Cylindrocarpon lichenicola* were placed in the group. Strain "*C. lichenicola*" (current name *Fusarium lichenicola*) was obviously incorrectly identified. The status of *A. lini* has been discussed above. Strain IFO 8984 *A. mali* was not ex-type. The same strain and the type strain of *A. mali* have been studied by Rotondo et al. (2012). The strains did not demonstrate a close relationship, but both do appear to be members of *A. tenuissima*/*A. alternata* group, which is placed in *A*. sect. *Alternaria*.

Woudenberg et al. (2013) added *Alternaria daucifolii* to *A*. sect. *Alternaria,* confirming 21 species (in addition to the type species) in the section. Also three putatively representative strains corresponding to the names *Clathrospora heterospora*, *Comoclathris magna*, and *Nimbya gomphrenae* were found to be closely related to species in *A*. sect. *Alternaria*. Presumably the strains *Clathrospora heterospora* (CBS 175.52) and *Comoclathris magna* (CBS 174.52) were lost during cultivation and were replaced by *A. alternata* group isolates (Woudenberg et al. 2013). A strain of *Nimbya gomphrenae* (CBS 108.27) was isolated by Togashi and deposited at CBS in 1927, but Simmons (1989) maintained that Togashi actually isolated two fungi, one the distinctive large-spored *A. gomphrenae* [≡ *N. gomphrenae*] and the other a small-spored, chain-forming species in the *A. alternata* group. This suggests that the strain used by J. Woudenberg et al. most likely is a contaminant.

Initially *A*. sect. *Alternaria* was estimated to comprise about 60 species (Gannibal 2012; Woudenberg et al. 2013). The number of species approved by phylogenetic species recognition approaches may differ from that revealed by morphological analysis, and it is very likely that a morphological concept would favor splitting. For instance, phylogenetic analyses were performed with 150 small-spored *Alternaria* isolates using sequence data from three genomic loci (Andrew et al. 2009). Strict congruence between morphology and phylogenetic lineage was not found among isolates morphologically defined as *A. alternata* or *A. tenuissima*. Although 5–9 well-supported clades were evident among isolates, it was unclear whether these clades should be considered phylogenetic species or emerging evolutionary lineages.

In other works (Peever et al. 2004, 2005) lineages inferred from phylogenetic analysis of the combined dataset were in general agreement with described morphospecies; however, three clades contained more than one morphological species. The authors agreed to collapse all morphologically diverse small-spored, citrus-associated isolates of *Alternaria* into a single phylogenetic species, *A. alternata*.

The main diagnostic morphological feature of many *Alternaria* sect. *Alternaria* species is short conidia (usually no longer than 60 µm in culture) produced in chains (Lawrence et al. 2013; Woudenberg et al. 2013). Sexual morphs have not yet been discovered. Many strains of most well-studied species produce toxic metabolites, such as derivatives of dibenzo-α-pyrone (alternariol, alternariol monomethyl ether, altenuen, etc.), tetramic acid (tenuazonic acid), and perylene (altertoxin I, II and III) (Andersen et al. 2001, 2002; Lou et al. 2013). Almost all species in this section are saprobes or facultative parasites of plants with no strong host specialization. Only a few species (or — in an alternative classification — pathotypes of *A. alternata*) are known to be strong but specialized parasites, each able to infect only a few genotypes (cultivars) of a host plant (Tsuge et al. 2013). Such species become pathogenic due to a limited group of genes associated with synthesis of host-selective toxins, but presumably they have all the same adaptations necessary for saprotrophic growth as seen in closely related species.

It is unlikely that all 280 *Alternaria* species will be molecularly characterized in the foreseeable future. Moreover, for several species living isolates are not known and herbarium material is too old and scanty for successful DNA extraction. On the other hand, the morphological diversity of *Alternaria* is well studied and available in a monograph (Simmons 2007), and classical comparative morphological approaches can still be utilized to assign all *Alternaria* species to sections.

This work continues the series begun with *A.* sect. *Porri* (Gannibal 2015). The aim of the present work is to detect which phylogenetically unexamined *Alternaria* species fit the current morphological circumscription of *A.* sect. *Alternaria* and to emend the morphological concept of this section.

Materials & methods

Morphology of almost all *Alternaria* species with legitimate names was analyzed with regard to conformity with criteria of *Alternaria* sect. *Alternaria*. The morphological assessment was based on descriptions made by Simmons (2007). As *A.* sect. *Alternaria* is the autonymous section including the genus type, it contains all species that have not yet been segregated into other sections or designated as INCERTAE SEDIS. In this article I consider only species that are phylogenetically or morphologically closely related to the type species and do not treat "omitted" or "obscure" species.

Results & discussion

Evaluation of all available descriptions of *Alternaria* species allowed for the addition of 37 species to *A.* sect. *Alternaria,* here recognized as comprising the 59 species listed in TABLE 1.

Table 1. List of the 59 *Alternaria* spp. assigned to *A.* sect. *Alternaria*

A. alocasiae T.Y. Zhang & M.X. Gao [a, b]

A. alternata (Fr.) Keissl. [= *A. tenuis* Nees] (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)

A. amorphophalli V.G. Rao [a]

A. angustiovoidea E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)

A. arborescens E.G. Simmons (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)

A. asclepiadea (Cooke) E.G. Simmons [a]

A. betae-kenyensis E.G. Simmons

A. brassicinae E.G. Simmons

A. broussonetiae T.Y. Zhang, W.Q. Chen & M.X. Gao

A. burnsii Uppal, Patel & Kamat (Lawrence et al. 2013; Woudenberg et al. 2013)

A. catharanthicola T.Y. Zhang [a, b]

A. caudata (Cooke & Ellis) E.G. Simmons

A. cerealis E.G. Simmons & C.F. Hill (Lawrence et al. 2013; Woudenberg et al. 2013)

A. citri Ellis & N. Pierce [a]

A. citriarbusti E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)

A. citricancri E.G. Simmons

A. citrimacularis E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)

A. colombiana E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)

A. daucifolii E.G. Simmons (Woudenberg et al. 2013)

A. destruens E.G. Simmons (Pryor & Bigelow 2003; Lawrence et al. 2013; Woudenberg et al. 2013)

A. dumosa E.G. Simmons (Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)

A. floridana (Cooke) E.G. Simmons [a]

A. franseriae E.G. Simmons [a]

A. gaisen Nagano ex Hara (Lawrence et al. 2013; Woudenberg et al. 2013)

A. godetiae (Neerg.) Neerg.

A. graminum (Cooke) P. Joly [a]

A. herbiphorbicola E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)

A. hesperidearum (E. Pantan.) E.G. Simmons

A. hibisci Bouhot ex E.G. Simmons [a]

A. interrupta E.G. Simmons

A. limoniasperae E.G. Simmons (Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)

A. longipes (Ellis & Everh.) E.W. Mason (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)

A. mali Roberts (Rotondo et al. 2012)

A. malvae Roum. & Letendre [a]

A. obclavoidea E.G. Simmons [a]

A. palandui Ayyangar

A. pellucida E.G. Simmons
A. perangusta E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)
A. petalicolor (Sorokin) E.G. Simmons [a]
A. platycodonis Z.Y. Zhang & H. Zhang
A. postmessia E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)
A. pulvinifungicola E.G. Simmons
A. rhadina E.G. Simmons [a]
A. rhizophorae E.G. Simmons
A. rugosa McAlpine [a]
A. sanguisorbae M.X. Gao & T.Y. Zhang
A. senecionicola E.G. Simmons & C.F. Hill
A. soliaegyptiaca E.G. Simmons
A. spadicea (Thüm.) E.G. Simmons [a]
A. tangelonis E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)
A. tenuissima (Kunze) Wiltshire (Pryor & Bigelow 2003; Hong et al. 2005; Lawrence et al. 2013; Woudenberg et al. 2013)
A. tinosporae E.G. Simmons
A. tomaticola E.G. Simmons & Chellemi
A. toxicogenica E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)
A. tropaeolicola T.Y. Zhang [a, b]
A. turkisafria E.G. Simmons (Lawrence et al. 2013; Woudenberg et al. 2013)
A. uredinis (Ellis & Barthol.) E.G. Simmons [a]
A. yaliinficiens R.G. Roberts
A. zhengzhouensis T.Y. Zhang [a, b]

Names with parenthetical annotations = species with phylogenetic data (in the cited references).
Bold font names = species assigned to *Alternaria* sect. *Alternaria* previously based on phylogenetic data (Lawrence et al. 2013 and/or Woudenberg et al. 2013 or Rotondo et al. 2012).
Unannotated names = species with reliable living cultures and herbarium specimens.
Names with square bracketed annotations = species for which type material and/or representative strains are not available: [a] = no known living isolates; [b] = type specimen is not available on loan.

The most complicated task was differentiating species of *A.* sect. *Alternaria* from species belonging to *A.* sect. *Infectoria* and *Pseudoalternaria.* Typical representatives of those two groups can easily be identified by a number of cultural and microscopic morphological features (Lawrence et al. 2014). But the intermediate morphology of several species or strains tends to blur the morphological border between these two groups.

Although molecular analyses and morphological observations coincide for most species, they are discordant in the case of *A. herbiphorbicola*. In this species the conidia are short (conidial body is mainly 15–22 μm long) and produce secondary conidiophores that can slightly exceed the length

of the body. The three-dimensional sporulation pattern resulting from such relatively long secondary conidiophores with several conidiogenous loci is similar to that of *Pseudoalternaria.* But in many *Pseudoalternaria* species a portion of conidia usually have longer apical secondary conidiophores (30–80 μm). In *Pseudoalternaria* lateral secondary conidiophores usually have 1–2 conidiogenous loci, while several species of *Alternaria* sect. *Alternaria*, including *A. herbiphorbicola*, can produce such conidiophores with up to 4 pores.

Despite ambiguities resulting from the lack of authentic living cultures, both *A. malvae* and *A. rhadina* should be placed in *A.* sect. *Alternaria* based on the morphological characters documented by Simmons (2007).

Here I emend (and somewhat expand) the description of *Alternaria* sect. *Alternaria* given previously by Lawrence et al. (2013). Characters are quantified when appropriate, and examples are provided for species whose quantified characters either depart from the section norm or conform to it.

Alternaria* Nees sect. *Alternaria emend. Gannibal

Type: *Alternaria tenuis* Nees [= *Alternaria alternata*]

On PCA primary conidiophores are straight or curved, simple or branched, short (15–60 μm; *A. brassicinae*, *A. gaisen*) or long (≤300–435+ μm; *A. betae-kenyensis*), 3-4 μm wide. Conidiophores bear one or several (ranging from 1–2 to 1–5 in different species) conidiogenous loci at the apex. Conidia form simple or branched chains that are moderately long (2–6 conidia; *A. godetiae*, *A. toxicogenica*) to long (10–20+ conidia; *A. daucifolii*, *A. perangusta*). Conidial aggregates usually present as simple straight to branched chains of conidia or as loose to tightly packed branching clusters (≤125 conidia; *A. alternata*). Young terminal conidia often are short ovoid or ellipsoid. Mature conidia are obclavate, long ellipsoid or ellipsoid, septate, 15–50(–60) × 7–13 μm in culture and somewhat larger in nature (long secondary conidiophores are not included in calculation). Conidia mainly distoseptate, with numerous transverse septa (ranging from 3–7 to 5–12 in different species) and 1–2 longitudinal septa in one or a few of the transverse divisions. In some species fully developed conidia have 1–3 eusepta. Conidia are slightly constricted near eusepta and sometimes near some distosepta. Most conidia narrow gradually into a tapered beak or secondary conidiophore. Apical secondary conidiophores are short, usually not exceeding 5–10 μm (but sometimes longer, in some species ≤100–110+ μm; *A. angustiovoidea*, *A. tinosporae*), bearing one to several conidiogenous loci (ranging from 1–2 to 1–4 in different species). Some conidia produce short solitary lateral secondary conidiophores. They are simple or with very short branches, 5–10(20)×3–4 μm, with 1-4 conidiogenous loci.

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